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EFFECTS OF PHOTOPERIOD AND TEMPERATURE ON GONADAL ACTIVITY IN THE CYPRINID TELEOST, *NOTEMIGONUS CRYSOLEUCAS*

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Recent literature reviews (de Vlaming, 1972a, 1974) indicate that there is considerable variation among teleost fishes with regard to environmental control of reproductive cycling. Photoperiod may exert the dominant regulatory role of sexual cycles in the salmonids and gasterosteids. Temperature appears to be extremely important in regulating reproductive rhythms in the cyprinodontiform fishes.

Daylength changes in combination with various temperatures seem to be important in controlling reproduction in the cyprinid and centrarchid fishes (*cf.* de Vlaming, 1972a, 1974). Champy (1923) suggested that warm temperature treatment in late autumn stimulates the completion of spermatogenesis in the cyprinid, *Phoxinis laevis;* the potential role of photoperiod in gonadal maturation or the possible seasonal change in response to temperature were not discussed. A later study (Bullough, 1939) with this species indicated that high temperatures promote the early phases of spermatogenesis and oogenesis, regardless of photoperiod. Bullough (1939) implied that long photoperiods are required for the final stages of gonadal maturation in *Phoxinus* captured in autumn. In a later study, Bullough (1940) reported that *Phoxinus* maintained under natural temperature conditions, but on a short photoperiod from autumn to spring underwent gonadal recrudescence by spring. Although temperatures increased in nature during this time, Bullough concluded that, since the short photoperiod did not prevent recrudescence, this minnow has an internal reproductive rhythm which acts independently of exogenous factors. Kawamura and Otsuka (1950) demonstrated that long photoperiods and warm temperatures during winter and spring result in sexual maturation in female goldfish, *Carassius auratus.* No attempt was made to determine the relative importance of these two environmental factors, or if there is a seasonal variation in responsiveness to photoperiod and temperature. Fenwick (1970) exposed goldfish to various photoperiods at several different times of the year. Long photoperiods stimulated gonadal maturation in *Carassius,* but only during spring. All of Fenwick's experiments were conducted at low temperatures so the effects of warm temperatures in combination with different photoperiods are not known. The data of Kawamura and Otsuka (1950) indicate, in fact, that long photoperiods can stimulate gonadal maturation in *Carassius* during the winter if temperatures are warm.

The bridle shiner, *Notropis bifrenatus* (another cyprinid), exposed to constant warm temperatures in autumn exhibited sexual maturation ahead of the natural cycle if treated with a long photoperiod, but not on a short photoperiod (Harrington, 1950, 1957). Since low temperature controls were not included in these

studies, no conclusions can be drawn as to whether the effect of long photoperiods is temperature dependent. Verghese (1967) reported that long photoperiod treatment in autumn brought *Cirrhina reba,* a subtropical cyprinid, into spawning condition. Verghese failed to mention the temperature conditions of the experiment, so the importance of temperature and the possible temperature dependency of photoperiodism is not known. Possible seasonal variation in gonadal responsiveness of *Cirrhina* to exogenous factors was not considered by Verghese.

In another cyprinid, the lake chub (*Couesius plumbeus*), low temperatures favor the meiotic phase (proliferation of spermatocytes) of spermatogenesis and high temperatures promote spermiation and proliferation of spermatogonia (Ahsan, 1966). Photoperiod alone does not stimulate any phase of spermatogenesis in *Couesius,* but at low temperatures short photoperiods have a slight acceleratory effect. In this species the meiotic and maturational stages of spermatogenesis can be exogenously stimulated only as the normal spawning season approaches. Although both photoperiod and temperature may be important reproductive regulatory factors in the cyprinid family, the lack of adequate controls in many experiments with minnows prohibit meaningful interpretation or generalizations. Furthermore, the effects of photoperiod and temperature on gonadal activity may vary with season. Unfortunately the seasonal aspect of exogenous regulation of teleost reproductive cycles has not been extensively examined.

The intent of the present investigation was to examine the effects of various photoperiod-temperature regimes on gonadal activity in the cyprinid, *Notemigonus crysoleucas,* during several different phases of the annual reproductive cycle.

Materials and Methods

Samples of *Notemigonus crysoleucas* were collected in ponds around the area of Menomonee Falls, Wisconsin (43°10′N) at several different times during the year and thus in different phases of the reproductive cycle. The reproductive cycle of this population of *Notemigonus* consists of a spawning season which extends from May through July. There is a postspawning season during August and September in which the gonads of this species are regressed. From October through February there is a gonadal preparatory period, in which spermatogonia proliferate slowly and spermatocytes appear in the testes. Vitellogenesis is initiated during this period. March and April can be referred to as the prespawning period; during this time final gonadal maturation occurs (*i.e.*, spermatozoa fill the testes and ovaries are distended with mature oocytes). Several fish from each nature sample were sacrificed and the gonads examined at the time of collection; these fish served as a reference for the experiments that followed. In the following discussion the fish sacrificed at the time of collection will be identified as initial controls.

Experimental fish were maintained under various photoperiod and constant temperature regimes (see results) in 114 or 285 liter tanks supplied with aerated and filtered dechlorinated tap water. Temperatures selected for these experiments are within the range normally experienced during the year in nature by this species. Illumination was a combination of incandescent and cool white fluorescent bulbs which gave a light intensity of 200 to 300 lux at the surface of each tank. Fish

were fed once a day *ad libitum* on a commercial fish food (Tetra-Min). All specimens of *Notemigonus* used in these studies weighed between 12 and 17 grams.

The effects of the photoperiod-temperature regimes on reproductive function were assessed by gravimetric and histological techniques. Fish were sacrificed by severing the spinal cord. Body weight and gonadal weight were recorded immediately after sacrifice. Gravimetric data are expressed in terms of the gonosomatic index (gonadal weight/body weight $\times$ 100) since gonadal size in this species depends on body weight. After weighing, gonads were fixed in Bouin's solution and embedded in paraplast for histological examination. Spermatogenesis and oogenesis were each separated into seven and six recognizable phases respectively (Table I) to facilitate quantitative evaluation of gametogenic activity. Stage IV (active vitellogenic phase) of the oogenesis categories refers to ovaries in which yolky oocytes with a diameter of 125 to 620 μ predominate. Since Stage IV encompasses such a large size range of yolky oocytes a system has been adopted to better differentiate ovaries in this phase of maturation. The diameter of the 25 largest yolky oocytes in ovaries categorized in Stage IV were measured. A mean oocyte diameter was then determined for the ovaries of each fish in Stage IV.

TABLE I

Criteria used for evaluating gametogenic activity in the gonads of Notemigonus.

Stage	Histological characteristics of testes
0	"Regressing testis." Seminiferous lobules characterized by large numbers of pynotic nests of degenerating cells. Germinal epithelium disorganized.
1	"Quiescent testis." Germinal epithelium consists of a few primary spermatogonia only. Seminiferous lobules small in diameter. Lumen of the lobules contain only few residual spermatozoa.
2	"Mitotic phase." Similar to Stage 1 except spermatogonia are more numerous and mitotic figures are observed in many spermatogonia.
3	"Meiotic phase." Germinal epithelium consists of spermatogonia and spermatocytes. Testicular lobules larger than in Stages 1 and 2.
4	"Spermiogenic phase." Similar to Stage 3 except spermatids appear in germinal epithelium and some spermatozoa present in lumen of lobules.
5	"Prespawning testis." Seminiferous lobules very large and distended with sperm.
6	"Postspawning testis." Seminiferous lobules small and devoid of most germ cells. Sperm duct expanded and containing residual sperm.
Stage	**Histological characteristics of ovaries**
I	"Regressing ovary." Atretic follicles predominate in the ovary.
II	"Oogonial proliferation phase." Ovary characterized by nonyolky oocytes. Granulosa not fully organized around developing oocytes.
III	"Early vitellogenic phase." Oocytes with yolk vesicles present only in the periphery of ooplasm; diameter 70 to 125 μ.
IV	"Phase of active vitellogenesis." Yolk vesicles appear throughout ooplasm; diameter 125 to 620 μ.
V	"Prespawning ovary." Ovary charcterized by oocytes with a diameter of greater than 620 μ.
VI	"Postspawning ovary." The ovary appears red in color. The tunica albuginea thick, highly vascularized and folded. Post-ovulatory follicles predominate in the ovary. Ovarian stroma appears disorganized, yet highly vascularized.

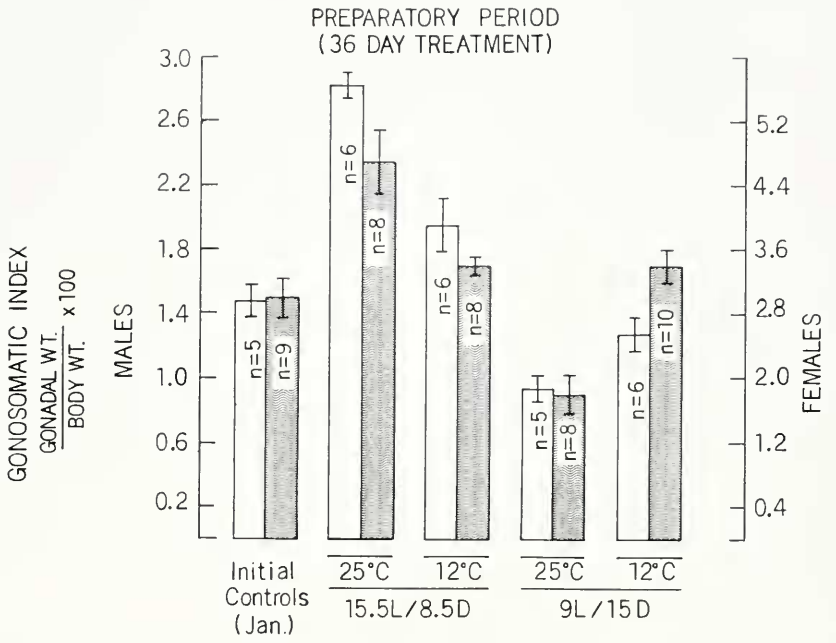

FIGURE 1. The effects of various photoperiod-temperature regimes on GSI in *Notemigonus* during the gonadal preparatory period. Initial controls refer to animals sacrificed at the time of collection. Histograms represent mean GSI; the mean is bracketed by one standard error. Testicular GSIs are shown by open histograms and ovarian GSIs by hatched histograms.

The mean yolky oocyte diameters from individual fish were averaged to obtain a mean and standard error for different experimental groups.

RESULTS

Preparatory season

The effects of various photoperiod-temperature regimes on gonadal activity in specimens of *Notemigonus* were first examined during January (late gonadal preparatory period). Fish were exposed for 36 days to a 15.5L/8.5D or 9L/15D photoperiod at either 25° or 12° C.

Testicular and ovarian GSIs increased significantly ($P < 0.01$) in fish maintained on the 15.5L/8.5D—25° C regime compared to the initial controls (Fig. 1). The testes of all initial controls were in the meiotic phase (Stage 3) of spermatogenesis (Table II). All male fish exposed to the long photoperiod-warm temperature regime advanced to the prespawning condition (Stage 5). Ovaries of the initial controls in January were in Stage III or IV (Table II). Three of the eight female fish maintained on the 15.5L/8.5D—25° C advanced to the prespawning condition (Stage V); the ovaries of the remaining fish in this group were in Stage IV (Table II). Stage IV oocytes in the ovaries of fish exposed to

TABLE II

Effects of various photoperiod and temperature regimes on gonadal activity in Notemigonus *during the preparatory period—36 day treatment (figures in this table refer to the number of fish in each group with gonads in a specific maturational stage).*

Treatment	Maturation stage of testes*						
	0	1	2	3	4	5	6
Initial controls (January)	0	0	0	5	0	0	0
15.5L/8.5D Photoperiod							
25° C	0	0	0	0	0	6	0
12° C	0	0	0	6	0	0	0
9L/15D Photoperiod							
25° C	3	0	2	0	0	0	0
12° C	2	0	4	0	0	0	0
	Maturation stage of ovaries*						
	I	II	III	IV		V	VI
Initial controls (January)	0	0	6	3(422 ± 16)[a]		0	0
15.5L/8.5D Photoperiod							
25° C	0	0	0	5(534 ± 23)[a]		3	0
12° C	5	0	2	3(500 ± 13)[a]		0	0
9L/15D Photoperiod							
25° C	5	3	0	0		0	0
12° C	0	0	4	6(431 ± 14)[a]		0	0

* See Table I.

[a] Mean diameter (±S.E.) in microns of 25 largest oocytes in each ovary.

the long photoperiod-warm temperature regime were significantly ($P < 0.05$) larger than in ovaries of the initial controls. These data indicate that a long photoperiod in combination with warm temperatures can promote final gonadal maturation in *Notemigonus* during the preparatory period.

Ovarian GSI in fish exposed to a long photoperiod at 12° C during the preparatory period did not differ significantly from the GSI of initial controls (Fig. 1). The ovaries of fish maintained on the 15.5L/8.5D—12° C regime were in Stages I, III or IV (Table II). Under these conditions testicular GSI increased significantly ($P < 0.05$) compared to the initial controls (Fig. 1). Testicular GSI in fish exposed to the 15.5L/8.5D photoperiod was significantly ($P < 0.05$) lower in the group at 12° C than in the group at 25° C. The testes of all fish exposed to the 15.5L/8.5D—12° C regime were in Stage 3 (Table II). Therefore, long photoperiod alone will not promote final gonadal maturation in *Notemigonus* during the preparatory period.

Ovarian and testicular GSIs decreased significantly ($P < 0.05$) in animals maintained on the 9L/15D—25° C regime compared to the initial controls (Fig. 1). Three of the male fish exposed to this regime were undergoing testicular regression (Stage 0) and the testes of the other two fish in this group were in Stage 2 (Table II). The ovaries of fish maintained on the 9L/15D—25° C regime

were regressing (Stage I) or in Stage II (Table II). Thus, warm temperature alone will not promote final gonadal maturation in *Notemigonus* during the preparatory period.

Neither ovarian nor testicular GSI of fish exposed to the 9L/15D—12° C regime differed significantly from the GSIs of the initial January controls (Fig. 1). Histological examination of the gonads of the animals maintained on this regime showed that they were in essentially the same phases of maturation as the gonads of the initial controls (Table II).

Early prespawning season

Specimens of *Notemigonus* collected in early March were exposed for 21 days to the four photoperiod-temperature regimes mentioned above.

Ovarian and testicular GSIs of fish maintained on the 15.5L/8.5D—25° C regime were significantly ($P < 0.05$) lower than those of the initial controls (Fig. 2). The testes of all of the initial controls were in Stage 3 (Table III). Two male fish exposed to the long photoperiod-warm temperature regime spawned; the testes of other males in this group were in Stage 3, 4 or 5. Possibly the two fish of this experimental group in Stage 3 spawned and reinitiated spermatogenesis. Female fish in the initial March controls were all characterized by ovaries in the vitellogenic Stage IV (Table III). Four of the eight female fish maintained on the 15.5L/8.5D—25° C regime spawned. The relatively low gonadal weights in animals maintained on the long photoperiod-warm temperature regime were un-

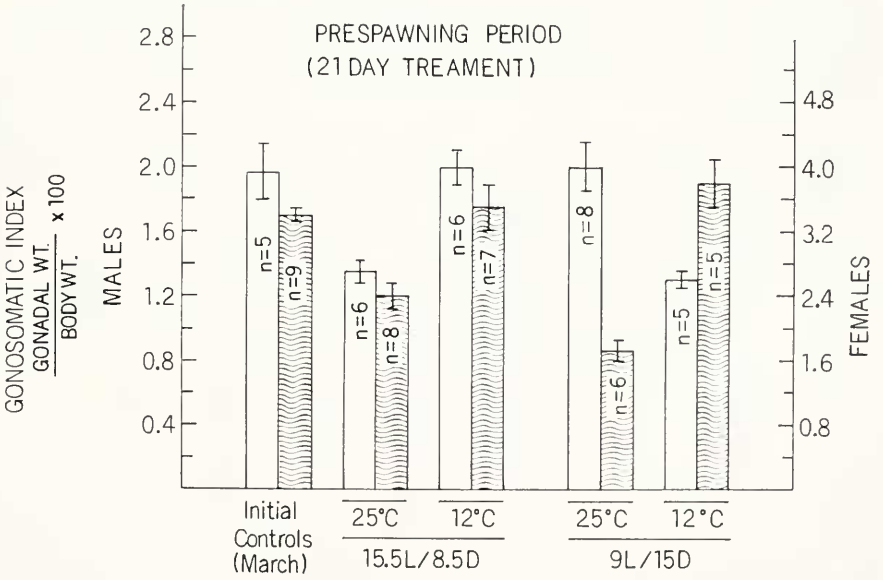

FIGURE 2. The effects of various photoperiod-temperature regimes on GSI in *Notemigonus* during the prespawning period. Initial controls refer to animals sacrificed at the time of collection. Histograms represent mean GSI; the mean is bracketed by one standard error. Testicular GSIs are shown by open histograms and ovarian GSIs by hatched histograms.

TABLE III

Effects of various photoperiod and temperature regimes on gonadal activity in Notemigonus *during the prespawning period—21 day treatment (figures in this table refer to the number of fish in each group with gonads in a specific maturational stage).*

Treatment	Maturation stage of testes*						
	0	1	2	3	4	5	6
Initial controls (March)	0	0	0	5	0	0	0
15.5L/8.5D Photoperiod							
25° C	0	0	0	2	1	1	2
12° C	4	0	0	2	0	0	0
9L/15D Photoperiod							
25° C	8	0	0	0	0	0	0
12° C	0	0	0	5	0	0	0
	Maturation stage of ovaries*						
	I	II	III	IV	V	VI	
Initial controls (March)	0	0	0	9(388 ± 16)[a]	0	0	
15.5L/8.5D Photoperiod							
25° C	0	0	0	2(531 ± 11)[a]	2	4	
12° C	0	0	1	6(443 ± 27)[a]	0	0	
9L/15D Photoperiod							
25° C	3	0	3	0	0	0	
12° C	0	0	0	5(418 ± 24)[a]	0	0	

* See Table I.

[a] Mean diameter (±S.E.) in microns of 25 largest oocytes in each ovary.

doubtedly due to spawning of some individuals in this group. These data further confirm that in combination with warm temperatures, long photoperiods stimulate final gonadal maturation and spawning in *Notemigonus*.

The 15.5L/8.5D—12° C regime did not cause significant changes in ovarian or testicular weights during the early prespawning period (Fig. 2). The testes of four of six fish maintained under these conditions regressed (Table III). Ovaries of a majority of the fish exposed to the 15.5L/8.5D—12° C regime were in Stage IV, as were those of the initial controls. Stage IV oocytes were, however, significantly ($P < 0.05$) larger in the experimental fish than in the initial controls (Table III).

Ovarian GSI was significantly ($P < 0.01$) lower in females maintained on the 9L/15D—25° regime than in initial controls (Fig. 2). Furthermore, the fish in this group were characterized by regressing ovaries (Stage I) or ovaries in Stage III (Table III). GSIs in male fish exposed to the short photoperiod-warm temperature regime and in initial controls were not significantly different (Fig. 2). Nonetheless, testicular regression (Stage 0) was occurring in all animals maintained on this regime (Table III).

GSIs of female fish acclimated to the 9L/15D—12° C regime and of initial controls did not differ significantly (Fig. 2). Moreover, ovarian activity in these

two groups did not differ appreciably as determined by histological examination (Table III). In specimens of *Notemigonus* exposed to the short photoperiod-low temperature regime testicular GSI was significantly ($P < 0.01$) lower than in initial controls (Fig. 2). The testes of all fish in 9L/15D—12° C experimental group and in the initial control group were in Stage 3; the lower testicular weights in the experimental group indicate that spermatogenic activity is in part suppressed by these conditions.

Early spawning season

The effects of various photoperiod-temperature regimes on gonadal activity were again examined in *Notemigonus* collected in late April (early spawning season). Animals were exposed for 21 days to a 15.5L/8.5D or 9L/15D photoperiod at either 25° or 15° C.

Ovarian and testicular GSIs did not differ significantly in the group maintained on the 15.5L/8.5D—25° C regime and in the initial controls (Fig. 3). In the initial controls, the testes of four of six fish were in the prespawning condition, whereas all fish exposed to the long photoperiod-warm temperature regime were

TABLE IV

Effects of various photoperiod and temperature regimes on gonadal activity in Notemigonus *during the early spawning period—21 day treatment (figures in this table refer to the number of fish in each group with gonads in a specific maturational stage).*

Treatment	Maturation stage of testes*						
	0	1	2	3	4	5	6
Initial controls (Late April)	0	0	0	0	2	4	0
15.5L/8.5D Photoperiod							
25° C	0	0	0	0	0	7	0
15° C	0	0	0	0	3	2	0
9L/15D Photoperiod							
25° C	0	0	0	1	4	0	0
15° C	0	0	0	0	6	0	0
	Maturation stage of ovaries*						
	I	II	III	IV		V	VI
Initial controls (Late April)	0	0	0	2(496)[a]		4	0
15.5L/8.5D Photoperiod							
25° C	0	0	0	0		4	3
15° C	0	0	0	3(489 ± 29)[a]		3	0
9L/15D Photoperiod							
25° C	0	0	5	4(453 ± 17)[a]		0	0
15° C	0	0	3	2(508)[a]		0	0

* See Table I.

[a] Mean diameter (±S.E.) in microns of 25 largest oocytes in each ovary.

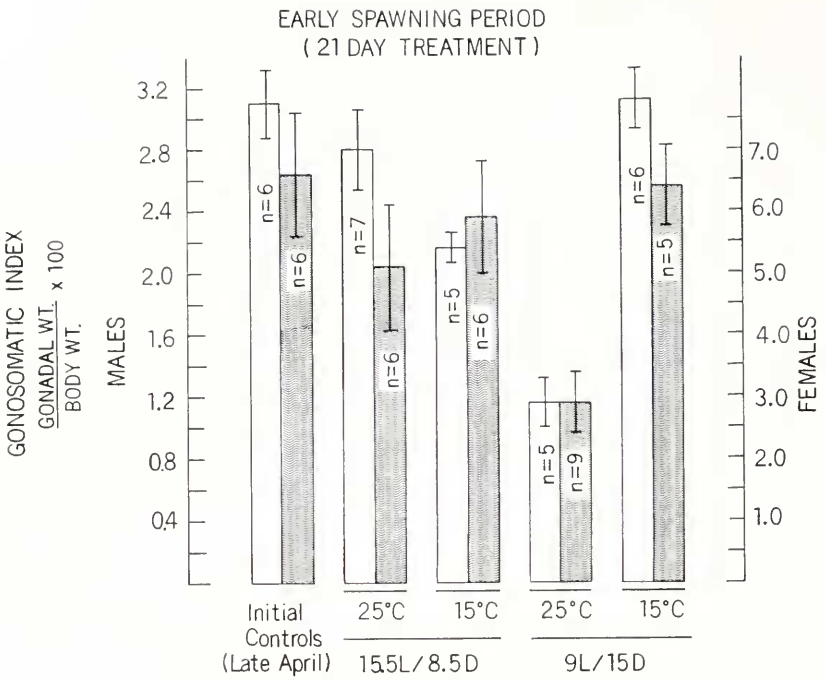

FIGURE 3. The effects of various photoperiod-temperature regimes on GSI in *Notemigonus* during the early spawning season. Initial controls refer to animals sacrificed at the time of collection. Histograms represent mean GSI; the mean is bracketed by one standard error. Testicular GSIs are shown by open histograms and ovarian GSIs by hatched histograms.

in the prespawning condition (Table IV). Four of the six female fish in the initial controls were also in the prespawning condition. Three of the seven female fish maintained on the 15.5L/8.5D—25° C regime spawned; the ovaries of the remaining animals in this group were in the prespawning condition (Table IV).

Testicular, but not ovarian GSI, was significantly ($P < 0.05$) lower in fish exposed to the 15.5L/8.5D—15° C regime than in initial controls (Fig. 3). Histological examination of the gonads of fish in the long photoperiod-low temperature group revealed that there were no striking differences in gametogenic activity compared to the initial controls (Table IV).

Both testicular and ovarian weights in the 9L/15D—25° C experimental group were significantly ($P < 0.01$) lower than in the initial controls (Fig. 3). The ovaries of five of the nine fish on the short photoperiod-warm temperature regime were in Stage III (Table IV). The testes of fish in this group were in Stage 3 or 4 (Table IV).

Neither ovarian nor testicular GSI in the animals maintained on the 9L/15D—15° C regime differed appreciably from GSIs of initial controls (Fig. 3). However, the ovaries of fish in the short photoperiod-low temperature group were in Stage III or IV (Table IV). The testes of all fish exposed to this regime were in Stage 4.

Postspawning season

Specimens of *Notemigonus* collected during mid-August (postspawning period) were exposed for 34 days to the photoperiod-temperature regimes mentioned above. Table V summarizes the changes in GSIs of fish maintained on these regimes.

Ovarian and testicular GSIs increased significantly ($P < 0.01$) in fish exposed to the 15.5L/8.5D—25° C regime compared to the initial controls (Table V). The ovaries of a majority of the initial controls were in a quiescent phase (Stage II), whereas those of females on the long photoperiod-warm temperature regime were in Stage IV or V (Table VI). Testes of initial controls were in Stage 1, 2 or 3; the 15.5L/8.5D—25° C regime stimulated the advancement of testicular development to Stage 4 (Table VI).

Testicular, but not ovarian GSI also increased significantly ($P < 0.01$) in animals exposed to the 15.5L/8.5D—15° C regime compared to the initial controls (Table V). Testes of all fish maintained on this regime were in Stage 4, whereas ovaries were in Stage III or IV (Table VI).

GSIs of both male and female *Notemigonus* exposed to a short photoperiod (at 25° and 15° C) were not significantly different from the GSIs of the initial controls. Histological examination of the gonads of fish exposed to a short photoperiod at either 25° or 15° C revealed that gametogenesis had not been stimulated under these conditions (Table VI).

Discussion

The data presented here indicate that both photoperiod and temperature are important factors in regulating sexual cycling in the cyprinid teleost, *Notemigonus crysoleucas*. Furthermore, the effects of various photoperiod-temperature regimes on gonadal activity in *Notemigonus* appear to vary with season (*i.e.*, the gonadal condition of the initial controls). During the preparatory period, an "out-of-season" long photoperiod-warm temperature regime stimulates testicular and

Table V

Effects of various photoperiod and temperature regimes on GSI in Notemigonus *during the postspawning period—34 day treatment.*

Treatment	Gonosomatic index $\frac{\text{Gonadal weight}}{\text{Body weight}} \times 100$			
	n	Males ($\bar{X} \pm$ S.E.)	n	Females ($\bar{X} \pm$ S.E.)
Initial controls (mid August)	8	0.47 ± 0.06	10	1.12 ± 0.16
15.5L/8.5D Photoperiod				
25° C	7	3.00 ± 0.21*	8	4.51 ± 0.44*
15° C	5	2.12 ± 0.17*	5	2.33 ± 0.63
9L/15D Photoperiod				
25° C	5	0.42 ± 0.07	5	1.32 ± 0.19
15° C	4	0.57 ± 0.14	5	1.43 ± 0.22

* Significantly ($P < 0.01$) different than in initial controls.

TABLE VI

Effects of various photoperiod and temperature regimes on gonadal activity in Notemigonus *during the postspawning period—34 day treatment (figures in this table refer to the number of fish in each group with gonads in a specific maturational stage).*

Treatment	Maturation stage of testes*						
	0	1	2	3	4	5	6
Initial controls (mid August)	0	2	4	2	0	0	0
15.5L/8.5D Photoperiod							
25° C	0	0	0	0	7	0	0
15° C	0	0	0	0	5	0	0
9L/15D Photoperiod							
25° C	0	2	2	1	0	0	0
15° C	0	0	2	2	0	0	0
	Maturation stage of ovaries*						
	I	II	III	IV		V	VI
Initial controls (mid August)	0	6	3	1(363)[a]		0	0
15.5L/8.5D Photoperiod							
25° C	0	0	1	4(396 ± 21)[a]		3	0
15° C	0	0	2	3(367 ± 14)[a]		0	0
9L/15D Photoperiod							
25° C	0	1	4	0		0	0
15° C	0	3	2	0		0	0

* See Table I.

[a] Mean diameter (±S.E.) in microns of 25 largest oocytes in each ovary.

ovarian development to the prespawning condition. Therefore, a long photoperiod in combination with warm temperatures is apparently required for final gonadal maturation in this species. Neither a long photoperiod alone nor a warm temperature alone induce gonadal development to the prespawning condition during the preparatory period. A long photoperiod-warm temperature regime also promotes sexual maturation in two other cyprinid fish, *Carassius auratus* (Kawamura and Otsuka, 1950) and *Notropis bifrenatus* (Harrington, 1950, 1957) during winter and spring. A combination of long photoperiods and warm temperatures are also required for final gonadal maturation in the centrarchid, *Lepomis cyanellus* (Kaya and Hasler, 1972). Other investigators (Bullough, 1939; Verghese, 1967) have suggested that long photoperiod treatment can stimulate "out-of-season" final gonadal maturation in cyprinids; these investigators, however, failed to mention the temperatures at which their experiments were conducted, so the relative importance of photoperiod and temperature cannot be determined.

During the prespawning and spawning seasons a warm temperature-long photoperiod regime stimulates spawning in *Notemigonus*. Long photoperiods alone or warm temperatures alone do not induce spawning during these periods. Apparently then, spawning in *Notemigonus* depends primarily on photoperiod and temperature conditions. In addition, these data suggest that a combination of a

long photoperiod and warm temperature are required for spawning. In the postspawning season a long photoperiod-warm temperature regime can induce spermiogenesis and stimulate development of ovaries to the prespawning condition. These data indicate that *Notemigonus* is not totally refractory to these conditions. In nature gonadal regression in *Notemigonus* occurs in late July and September when environmental temperatures are warm, but when daylength begins to decrease. Potentially then, *Notemigonus* could continue to breed if daylength did not decrease.

Short photoperiods or decreasing daylength in combination with warm temperatures may induce gonadal involution in *Notemigonus*. In fact, short photoperiod-warm temperature treatment did result in gonadal regression in *Notemigonus* during the preparatory and prespawning periods. The gonadal regression response to a warm temperature-short photoperiod regime was not, however, observed during the spawning and postspawning periods. During these periods exposing *Notemigonus* to a short photoperiod-warm temperature regime did not stimulate advancement to the prespawning condition, but did promote spermatocyte proliferation and the initiation of vitellogenesis. These observations are consistent with environmental data because spermatocyte proliferation and the initiation of vitellogenesis do occur in early fall. It appears, therefore, that the early phases of gametogenesis are independent of environmental factors (more evidence for this hypothesis is presented below). The potential role of environmental factors in controlling gonadal regression in teleosts has received very little attention. In *Gillichthys mirabilis* (de Vlaming, 1972b) and *Lepomis cyanellus* (Kaya, 1973) high temperatures induce gonadal regression.

Long photoperiods in the absence of warm temperature do not promote final gonadal maturation in *Notemigonus*. A long photoperiod in combination with a low temperature maintains vitellogenesis during all seasons in *Notemigonus*, but does not promote final ovarian maturation or spawning. Therefore, long photoperiods alone cannot induce final oocyte maturation in this species. During the preparatory and prespawning seasons a long photoperiod-low temperature regime is not effective in stimulating spermiogenesis in *Notemigonus*. During the spawning and postspawning periods this regime maintains gametogenesis, but does not promote final testicular maturation. These data indicate that the effects of a long photoperiod-low temperature regime on gonadal development in *Notemigonus* vary with season, yet these conditions will never stimulate final gonadal maturation or spawning.

A short photoperiod-low temperature regime is effective in maintaining vitellogenesis at all times of the year in *Notemigonus*. Final ovarian maturation, however, will not occur in fish maintained under these conditions. During the preparatory, prespawning and postspawning seasons a low temperature-short photoperiod regime promotes spermatogonial and spermatocyte proliferation, but not spermiogenesis. Thus these conditions do not retard the early phases of gametogenesis in this cyprinid.

Combined, the results of these experiments indicate that spermiogenesis and vitellogenesis are independent of environmental control in *Notemigonus*, but spermiation and final oocyte maturation depend on a combination of long daylengths and warm temperatures.

The effects of various photoperiod and temperature regimes on gonadal activity in *Notemigonus* probably result from changes in pituitary gonadotropin secretion. Indeed, pituitary gonadotropin potency did vary in animals maintained under different regimes (de Vlaming, unpublished results). In *Notemigonus* hypothalamic gonadotropin releasing activity is significantly greater in fish exposed to a warm temperature-long photoperiod regime than in animals maintained on a warm temperature-short photoperiod regime (de Vlaming, unpublished results). The long photoperiod condition is also effective in stimulating spawning, whereas the short photoperiod regime results in gonadal regression. The effects of daylength on gonadal activity in *Notemigonus* thus seem to be mediated via the hypothalamus.

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Summary

1. The effects of various photoperiod-temperature regimes on gonadal activity in the cyprinid teleost, *Notemigonus crysoleucas*, were examined during several different phases of the annual reproductive cycle.

2. Regardless of the time of year when the experiment is initiated a long photoperiod-warm temperature regime stimulates gonadal development to the prespawning condition or induces spawning. Neither a warm temperature alone nor a long photoperiod alone will stimulate final gonadal maturation.

3. *Notemigonus* is not "refractory" to long photoperiod-warm temperature gonadal activation during the postspawning season.

4. Short photoperiods in combination with warm temperatures cause gonadal regression in this species. A low temperature-short photoperiod regime does not induce gonadal involution.

5. Spermatocyte formation and proliferation as well as the early phases of vitellogenesis occur independently of environmental factors. Final gonadal maturation and the rate of gametogenesis, however, depend on specific environmental conditions.

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